Agricultural and Forest Meteorology 263 (2018) 258–266

Contents lists available at ScienceDirect

Agricultural and Forest Meteorology

journal homepage: www.elsevier.com/locate/agrformet

Coupling transversal and longitudinal models to better predict *Quercus petraea* and *Pinus sylvestris* stand growth under climate change

Patrick Vallet[a,b,*], Thomas Perot[b]

[a] Univ. Grenoble Alpes, Irstea, UR LESSEM, 2 rue de la Papeterie - BP 76, 38402 St-Martin-d'Hères, France
[b] Irstea, UR EFNO, Domaine des Barres, 45290 Nogent-sur-Vernisson, France

ARTICLE INFO

Keywords:
Temperate forest
Growth modeling
Climate change
National forest inventory
Dendrochronology
Space-for-time substitution

ABSTRACT

Climate change has swept away the former general principles of long-term stability in forest productivity. New types of models are needed to predict growth and to plan forest management under future climate conditions. These models must remain robust for silvicultural practices and variations in climate. In this study, we present a new type of model development to achieve these goals.

Our study focused on pure and mixed stands of *Quercus petraea* and *Pinus sylvestris* in central France. We used National Forest Inventory (NFI) data: respectively, 525 and 548 pure plots of *Quercus petraea* and *Pinus sylvestris*, and 68 plots of mixed species. We also used 108 tree cores from an experimental site of the same species. The cores cover the period from 1971 to 2013, making a total of 4572 individual annual increments.

We coupled two types of models. One was developed with NFI data (transversal data). This model takes into account mean diameter and stand density effects on stand growth. It includes a set of biophysical factors accounting for stand fertility. The other one was developed with the data from tree cores (longitudinal data), and provides a climate modulation thanks to the correlation between ring width and yearly climate. The model with tree core data reveals the influence of December to July rainfalls on yearly variability in stand growth for *Quercus petraea* and of May to August rainfalls for *Pinus sylvestris*.

We obtained a coupled model that allowed us to project growth up to 2100 for all the different IPCC scenarios but one; the model was outside its area of validity beyond 2060 for the RCP 8.5 scenario.

1. Introduction

Forest management has traditionally been based on concepts, tools or rules representing the long-term stability of forest productivity. Yield tables were common tools that allowed foresters to plan for changes in wood volumes and harvesting strategies (Assmann, 1970). Empirical forest dynamics models and simulators then replaced yield tables (Dufour-Kowalski et al., 2012). Even if these newer tools are more accurate and flexible, the general underlying principles of stability in forest evolution over time remain. Climate change, as well as nitrogen deposition rates or changes in CO_2 concentrations, has now swept away the temporal stability of forest productivity (Pretzsch et al., 2014), and new tools are needed to plan for forest productivity according to different climatic scenarios. Process-based models are interesting options to take climate change into account (Fontes et al., 2010). Their ability to break processes down and link them to climate factors – especially water availability and temperature – allows us to predict changes in growth under yet-to-exist climate conditions for a given species. Empirical models based on long-term stand monitoring are more efficient to take stand density and the structure of individual trees into account than process-based models linked to physiological mechanisms and running at the organ level. Hybrid models are interesting options: they are made to be easy to parameterize and make it possible to assess stand-level management and silvicultural practices but still accounting for the key mechanisms driving individual tree growth, regeneration and mortality (Pretzsch et al., 2008; Fontes et al., 2010).

Recent attempts to add a stand structure module to a process-based model has given promising results related to density and individual-tree distribution effects (Guillemot et al., 2014). Hybridization in the other direction, consisting in adding a climate modulation module to an empirical model based on long-term dendrometric observation, has rarely been undertaken. Yet, this option is promising to take both silvicultural practices and climate effect into account, and requires few input parameters.

The wide range of site conditions, silvicultural treatments and development stages encountered in National Forest Inventory data makes

* Corresponding author at: Irstea, UR LESSEM, 2 rue de la Papeterie, BP 76, F-38402 St-Martin-d'Hères, France.
E-mail address: patrick.vallet@irstea.fr (P. Vallet).

https://doi.org/10.1016/j.agrformet.2018.08.021
Received 6 April 2018; Received in revised form 21 August 2018; Accepted 22 August 2018
Available online 06 September 2018
0168-1923/ © 2018 Elsevier B.V. All rights reserved.

Table 1
Description of the NFI dataset. Min and max values in parenthesis.

	Number of plots	Mean annual temperature (°C)	Mean annual precipitation (mm)	Elevation (m)	*Q. petraea* mean diameter (cm)	*Q. petraea* mean basal area (m2/ha)	*P. sylvestris* mean diameter (cm)	*P. sylvestris* mean basal area (m^2/ha)
Q. petraea pure plots	525	10.4 (7.2–12.7)	785 (589–1673)	226 (20–1466)	32.3 (3.3–87.7)	17.9 (0.3–48.1)	– –	– –
Pinus sylvestris pure plots	548	8.8 (4.8–13.1)	920 (500–1727)	833 (37–1866)	– –	– –	22.5 (1.6–59.0)	20.3 (0–67.6)
Mixed plots	68	10.0 (8.1–11.3)	757 (604–1456)	243 (105–869)	26.3 (7.4–78.3)	9.7 (0.4–32.4)	34.6 (11.1–61.2)	14.8 (1.7–41.8)

it possible to develop robust models that take all these factors into account (Río and Sterba, 2009; Toïgo et al., 2015a, 2018). Thanks to the large-scale of such transversal data, the effect of climate on forest productivity can be revealed along spatial climate gradients. Considering spatial climatic effects instead of temporal variations in climate is call space-for-time substitution. However, several authors (Elmendorf et al., 2015; Roitberg and Shoshany, 2017) have shown that space-for-time substitutions could overestimate the climatic warming effect. Substituting space for time could be especially misleading when the climate effect on processes under study are weak compared to biotic interactions (Dunne et al., 2004).

Conversely, data from tree cores allow us to study the effect of temporal variations in climate on tree growth, as ring width is a reliable marker of past climate (Sheppard et al., 2002; Toïgo et al., 2015b). Analyzing past ring widths along with past climatic data makes it possible to include the effect of yearly climatic variations in growth models. However, in these dendrochronological studies, stand structure and density are generally unknown, which precludes including these parameters in dendrochronological models.

The aim of our study was to develop a new type of hybrid model, taking advantage of two types of observational data, i.e. NFI and tree cores. In a first step, we developed large-scale stand growth-models from National Forest Inventory data. These models integrate the effects of silvicultural practices as well as the site index using the biophysical factor (including mean climate of the stand). In a second step, we used tree cores to model the variation on stand growth induced by annual fluctuations of climate. Next, we built a link function between the two model types to obtain our coupled growth model. Finally, we used this growth model, which now included climatic effects, to simulate future growth under different climate-change scenarios up to the year 2100 (IPCC, 2013). We developed our method on pure and mixed stands of *Quercus petraea* and *Pinus sylvestris,* two widespread species in France and in Europe. Concerns exist about the ability of these two species to face to climate change in these regions. Cheaib et al. (2012) have shown a severe loss of their potential distribution area, whereas these species are of great importance for the forestry sector.

2. Materials and methods

2.1. Large scale models

2.1.1. National Forest Inventory data

The field plots monitored by the French National Forest Inventory (NFI) are systematic temporary plots located on a 1 km x 2 km grid. Every year, about on tenth of the plots are measured, about 6000 to 7000 plots a year. Each plot is made up of three circles 6 m, 9 m, and 15 m in radius, where small, medium and large trees are measured (respectively, trees with circumferences > 23.5 cm and < 70.5 cm, > 70.5 cm and < 117.5 cm, and > 117.5 cm). Data recorded include species, circumference, the last five years' radial increment taken from a core sample and total height. Soil is described on each plot, and a floristic survey is carried out; this makes it possible to assess pH or carbon-to-nitrogen ratio with bio-indication models (Gégout et al., 2005). We applied the Aurhely model from the French Meteorological Service to the coordinates of the NFI plots to obtain 30-year mean monthly climatic data (temperature and precipitation) for the 1961–1990 period (Bénichou and le Breton, 1987). These averaged climate data are used to differentiate climate across space in NFI models.

We used data from the 2006 to 2012 annual campaigns, which are freely available on the French NFI website (https://inventaire-forestier.ign.fr/). We selected pure and mixed plots according to several criteria. For pure stands, we selected plots where 100% of the basal area was of the target species (*Quercus petraea* or *Pinus sylvestis*). For mixed stands, we selected plots where the sum of the two species was over 80% and where the total basal area of all other species was below that of either *Quercus petraea* or *Pinus sylvestris*. We focused our study on plots with only one dominant layer. We also discarded plots that had been subjected to thinning during the previous five years to avoid changing density conditions being reflected in the measured increments. Finally, to include as many different environmental conditions as possible in our data set, we did not apply any geographical criterion to select our pure stands. However, we did apply a geographical criterion for the mixed plots: we wanted to be able to apply the pure stand model to the mixed plots to assess the basal area productivity that would be expected if they were in pure stand conditions. Therefore, mixed plots had to be within the range of pure stands site conditions, even though environmental factors reflecting those conditions were included in the model. We therefore only selected mixed plots in areas with enough pure plots to calibrate the pure stand model; we discarded any "silvo-ecological-region" defined by the French NFI (IFN, 2011) with less than five pure plots.

Finally, we obtained a dataset made up of 525 pure stands of *Quercus petraea*, 548 pure stands of *Pinus sylvestris* and 68 mixed stands with the two species (Table 1).

2.1.2. Modeling framework

We modeled stand basal area increment over five years for both species using the approach developed in previous studies based on French NFI data (Vallet and Perot, 2011; Toïgo et al., 2015a, 2018). The model takes the form of potential x reducer. The potential depends on site conditions, one reducer depends on the density of the stand and a second reducer depends on the quadratic mean diameter of the species (Eq. (1)).

$$BAI = \left(a_0 + \sum_{m=1}^{n} (a_m X_m)\right) \times (DI^b) \times \left(\frac{e^{(c_1 Dg)} + c_2}{1 + c_2}\right) + \varepsilon \quad (1)$$

where BAI is the basal area increment ($m^2.ha^{-1}$) of the trees in the overstorey, DI is the density index based on a self-thinning boundary calculated for the NFI dataset (Eq. (2)) (Condés et al., 2017; Toïgo et al., 2018), and Dg is the mean quadratic diameter of the stand (cm). DI and Dg are values at the beginning of the increment period (calculated using circumference measurements minus increment value). X_m is a set of n environmental variables limiting the growth of the species (mean monthly climatic variables, soil or stand description variables, elevation, etc. The full list is given in appendix A). We selected the variables

one after the other, including in the model at each step the environmental variable that lowered the most the Akaike Information Criterion (AIC), until no more variable had a significant effect. We did not selected variables correlated to previously included variables.

$$DI = \sum_i DI_i = \sum_i \frac{N_i}{N_{max,i}} = \sum_i \frac{N_i}{exp(d_{1,i} + d_{2,i} \times log(Dg_i))} \quad (2)$$

where i stands for species, N_i and Dg_i are respectively the stem number and the mean quadratic diameter of species i, and $d_{1,i}$ and $d_{2,i}$ are the parameters given in Toïgo et al. (2018) for each species.

We then calculated the mixture effect on productivity following the same method as in previous studies (Vallet and Perot, 2011; Toïgo et al., 2018). We applied the pure stand models to the mixed stands to estimate the expected basal area increment for each species i ($BAI_{expected,i}$) if these species had grown alone on the same site. We then analyzed the deviation from observed basal area increments (Eq. (3)).

$$Mixture\ effect_i = \frac{BAI_{observed,i} - BAI_{expected,i}}{BAI_{expected,i}} \quad (3)$$

where $BAI_{expected,i}$ is the basal area increment given by the model in pure stands, multiplied by the proportion of the target species i (Eq. (4)). The mixture proportion of a given species (p_i) was calculated as the ratio between the density index of the species (DI_i) and the total density index (DI) (Eq. (5)).

$$BAI_{expected,i} = \hat{BAI}_i \times p_i \quad (4)$$

$$p_i = DI_i / DI \quad (5)$$

Finally, the mixture effect was modeled as a linear function of the mixture proportion (Eq. (6)), as in previous studies (Vallet and Perot, 2011; Toïgo et al., 2015a, 2018). This model well fitted the data, and ensured continuity between the mixed and pure plots: when the mixture proportion tends toward pure ($p_i = 1$), the mixture effect tends toward zero.

$$Mixture\ effect = me_i \times (1 - p_i) \quad (6)$$

where p_i is the proportion of species i in the mixture, and me_i a parameter to be fitted.

2.2. Longitudinal climate-dependent models

2.2.1. Longitudinal data

OPTMix is a long-term experimental project (Korboulewsky et al., 2015) designed to better understand the functioning of adult *Quercus petraea* and *Pinus sylvestris* pure and mixed stands. The part of OPTMix used in this study consists of 9 stands: 3 repetitions of triplets of pure *Quercus petraea*, pure *Pinus sylvestris* and a mixed stand of both species. The OPTMix site is located in central France, in the Orléans State Forest (47°49′N, 2°29′ E). Elevation ranges from 107 m to 174 m above sea level. The soil is relatively poor and acidic with a sandy clay-loam texture (planosol, IUSS Working Group WRB, 2015). Superimposed layers of clay and sand lead to a temporary perched water table in winter, but low soil water storage capacity reduces the water available for plants in summer. The area has a temperate continental climate with an oceanic influence: mean annual temperature is 10.8 °C and mean annual rainfall is 729 mm (1981–2010 data from the SAFRAN and ISBA analytical platforms, Météo-France (Durand et al., 1993)). The stands were selected to have similar soil, age and dendrometric conditions (Korboulewsky et al., 2015).

During the 2012 and 2013 winters, in each of the nine stands, nine trees per species in each diameter class were felled for a study on drought resistance and resilience (Merlin et al., 2015). This provided a stratified sampling of 108 trees: two species (*Quercus petraea* and *Pinus sylvestris*) x two compositions (pure or mixed) x three triplet repetitions x nine trees of all sizes. Stem disks were taken at 1.30 m in height and were analyzed in the lab to reconstruct each individual's annual basal area increment (see Merlin et al. (2015) for full details of methods and checks). We discarded ring width data before the year 1970 to exclude juvenile growth. The description of the final dataset is given in Table 2.

Table 2
Description of the longitudinal tree sampling. Min and max values in parenthesis.

	Quercus petraea		*Pinus sylvestris*	
	Pure stands	Mixed stands	Pure stands	Mixed stands
Number of trees	27	27	27	27
Age at 1.30 m (yr)	64.8 (43–72)	68.6 (55–81)	55.7 (50–63)	62.4 (48–76)
Dbh (cm)	20.1 (11.6–30.6)	21.1 (11.8–35.7)	32.2 (22.3–41.4)	32.0 (20.7–47.7)
Number of observations (ring widths)	1143	1143	1143	1143

2.2.2. Modeling framework

The tree cores allowed us to study the relationship between the diameter of the trees and their basal area increment for every stand and for every year. Fig. 1 gives an example for *Quercus petraea* for one stand and for three years. This kind of linear relationship is classical in tree-growth modeling (Dhôte, 1999; Deleuze et al., 2004; Guillemot et al., 2014). The line can be defined with a threshold and a slope as in Eq. (7).

$$bai_t = \gamma \times (diameter_t - \alpha) \quad (7)$$

where bai_t is individual basal area increment for tree t, $diameter_t$ is the diameter of tree t, α is the threshold, and γ is the slope of the relationship. In the supplementary material, appendix B gives the relationship for every year and every stand for *Quercus petraea* (figure B.1) and *Pinus sylvestris* (figure B.2).

The observations were not independent. There are 42 (or 43) measurements of ring widths for a given tree (from years 1971–2012 (or 2013)). Moreover, the nine trees of a given stand are not independent either as they had the same management history. To take this structure into account, we included random effects in the model: both α and γ had a stand-level random effect, and α had a year random effect. Finally, we modeled the changes in these parameters with respect to stand age, a given year's climate and stand composition (pure or mixed). The effects of climate and stand composition were significant only on slope γ. Therefore, the final form of the model was as follows (Eq. (8)):

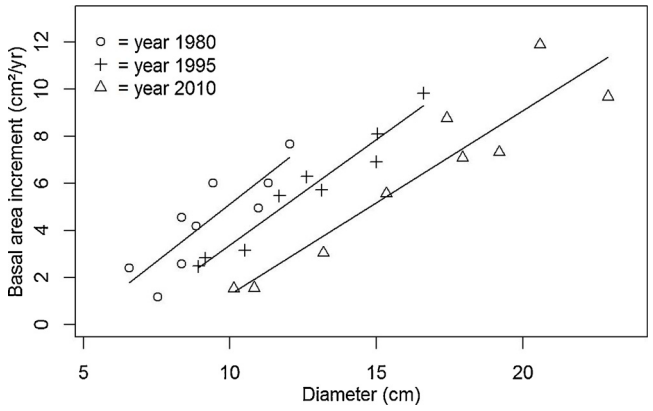

Fig. 1. Example of diameter x basal area increment relationship for *Quercus petraea* for one stand and for three years (1980, 1995 and 2010).

$$bai_{t,n,s} = ((\gamma_0 + \gamma_s) + \gamma_1 \times clim_n + \gamma_2 \times age_{n,s} + \gamma_3 \times comp_s + \gamma_4 \times clim_n \times comp_s) \times (diameter_{t,n,s} - ((\alpha_0 + \alpha_s + \alpha_n) + \alpha_1 \times age_{n,s})) \quad (8)$$

where the indices t, s, and n respectively represent tree, stand and year. γ_s and α_s are the stand random effect, α_n is the year effect, clim is the climate variable, age is the age of the stand for a given year, and comp is a Boolean variable (1 for mixed stands, 0 for pure stands).

We defined a large set of climate variables. We calculated all possible combinations of at least two consecutive months from October of the previous year to September of the growing year. For these periods, we calculated minimum, mean and maximum temperatures, cumulative precipitation, cumulative potential evapotranspiration and water balance (precipitation minus evapotranspiration). We ran model 8 with all the above-mentioned climate variables and selected as the best climate for each species the one with the lowest Akaike Information Criterion (AIC). We then added a second climate variable to the model following the same method. None of the second variables were significant.

2.3. Coupling method

The longitudinal model predicts individual tree increments within a stand. For a given stand, stand basal area increment (BAI_{long}) is the sum of the individual increments of all the trees within the stand:

$$BAI_{long} = \sum_t bai_t$$

bai_t is given by Eq. (7), where the slope does not depend on tree features.

$$BAI_{long} = \sum_t (\gamma \times (diameter_t - \alpha)) = \gamma \times \sum_t (diameter_t - \alpha)$$

Therefore, if we compare the basal area increment of a stand for a given climate ($clim_1$) to its basal area increment for another climate ($clim_2$), we obtain the following simplified formula.

$$\frac{BAI_{long,clim_1}}{BAI_{long,clim_2}} = \frac{\gamma_{clim_1} \times \sum_t (diameter_t - \alpha)}{\gamma_{clim_2} \times \sum_t (diameter_t - \alpha)} = \frac{\gamma_{clim_1}}{\gamma_{clim_2}}$$

On the other hand, we calibrated the large-scale NFI model with data for a given period and a given climate (hereafter, reference climate). This model represents the mean stand growth for the reference climate and depends on the diameter and the density of the stand. The mean stand growth for another climate would differ from the same stand growth with the reference climate. The coupling method between the two models relies on the assumption that the growth ratio between two periods was the same when calculated with the NFI model or with the longitudinal model. Therefore,

$$\frac{BAI_{NFI,clim}}{BAI_{NFI,clim_ref}} = \frac{BAI_{long,clim}}{BAI_{long,clim_ref}} = \frac{\gamma_{clim}}{\gamma_{clim_ref}}$$

We thus obtained the following coupled model:

$$BAI_{NFI,clim} = \frac{\gamma_{clim}}{\gamma_{clim_ref}} \times BAI_{NFI,clim_ref} \quad (9)$$

where $BAI_{NFI,clim_ref}$ is the stand basal area increment given by the NFI model, clim_ref is the climate during the calibration years of the NFI model, and γ_{clim} and γ_{clim_ref} are the slopes given by the longitudinal model for the predicted year's climate and the reference year's climate.

The ratio γ_{clim} over γ_{clim_ref} is therefore a modulation of the reference growth induced by climate. We can calculate it as a percentage of $BAI_{NFI,clim_ref}$.

$$climate\ modulation = \frac{\gamma_{clim}}{\gamma_{clim_ref}} \times 100 \quad (10)$$

As the NFI model was calibrated with data covering several years, and as the tree increment data were for five years, the reference is a combination of several years. Nonetheless, the simplifications resulting in Eq. (9) remain the same (see Appendix D). In the case of several years, γ_{clim_ref} becomes:

$$\gamma_{clim_ref} = \frac{1}{m} \times \sum_m \gamma \quad (11)$$

where m is the number of years of the reference, and γ is the slope given by Eq. (8).

The complete formulation of the final model is shown in appendix D.

2.4. Future climate data

Projections were calculated to evaluate the productivity of *Quercus petraea* and *Pinus sylvestris* with future climatic conditions. We used the climatic projections from the ALADIN high resolution numerical weather prediction model, available on the Drias website: http://www.drias-climat.fr/. We selected the projection plot the closest to the OPTMix experiment. Four datasets are available: one corresponding to historical data from 1950 to 2005, and three datasets corresponding to the IPCC scenarios RCP2.6, RCP4.5 and RCP8.5 from 2006 to 2100 (IPCC, 2013).

2.5. Statistical analyses

All the models were fitted with the R software version 3.3.2 and the *nlme* package (Pinheiro et al., 2015). The NFI models were fitted with the *gnls* function, which makes it possible to weight the observations with a power function of the fitted values. The longitudinal climate-dependent models were fitted with the *nlme* function to include random effects. We then added a variance model as a power of the diameter of the trees. We used the maximum likelihood method to compare the models and the restricted maximum likelihood method to fit the final model.

3. Results

3.1. NFI large-scale models

Both species had higher stand basal-area increment with smaller diameters and higher stand density. *Quercus petraea* was positively influenced by minimum December temperature, nitrogen content (Ellenberg index) and water holding capacity, and negatively influenced by July water deficit and limestone bedrock (Table 3). *Pinus sylvestris* was positively influenced by soil water holding capacity, and negatively influenced by increasing pH, July maximum temperature and steeper slope. Moreover, for *Pinus sylvestris*, we had a geographical remaining effect, taken into account through a Boolean variable (Table 3). We remind that for NFI large-scale models, the climatic variables are 1961–1990 averages allowing differentiating climate across space.

We did not find any mixture effect on productivity, either for *Pinus sylvestris* (p-value = 0.68) or for *Quercus petraea* (p-value = 0.076).

3.2. Longitudinal climate-dependent models

Of all the calculated climate variables included in the slope of the relationship, precipitation lowered AIC the most for both *Quercus petraea* and *Pinus sylvestris*. For *Quercus petraea*, it was the cumulative precipitation from December to July, whereas for *Pinus sylvestris* it was the cumulative precipitation from May to August. The appendix E shows the AIC for all the models including a precipitation variable; the AIC for the other variables were higher. For *Quercus petraea*, there was an interaction between precipitation and mixture: the slope γ was 24% higher in mixed stands. For both species, the threshold α increased with

Table 3
Statistical parameters (estimates, standard deviations, and p-values) of the NFI basal-area-increment models for pure *Quercus petraea* and pure *Pinus sylvestris* (Eq. (1)).

Species	Factor	Unit	Parameter (Eq. (1))	Est.	SD	p-value
Quercus petraea	Intercept	–	a_0	16.44	4.35	$< 10^{-3}$
	December min temperature	(°C)	a_1	3.56	0.62	$< 10^{-3}$
	July water deficit	(mm)	a_2	−0.188	0.042	$< 10^{-3}$
	Nitrogen index (Ellenberg)	–	a_3	3.26	0.70	$< 10^{-3}$
	Limestone bedrock	(Boolean)	a_4	−7.90	1.80	$< 10^{-3}$
	Soil water holding capacity	(mm)	a_5	0.80	0.16	$< 10^{-3}$
	Stand density	–	b_1	0.606	0.024	$< 10^{-3}$
	Mean diameter	(cm)	c_1	−0.1134	0.0056	$< 10^{-3}$
	Mean diameter	(cm)	c_2	0.0619	0.0052	$< 10^{-3}$
	Degrees of freedom	525				
	Power of the variance function	1.04				
	RMSE	0.331				
Pinus sylvestris	Intercept	–	a_0	152	26	$< 10^{-3}$
	pH	–	a_1	−5.81	1.10	$< 10^{-3}$
	Max July temperature	(°C)	a_2	−2.94	0.60	$< 10^{-3}$
	Slope	(%)	a_3	−0.210	0.047	$< 10^{-3}$
	Soil water holding capacity	(mm)	a_4	0.084	0.028	3.10^{-3}
	Geographical Unit (Semi continental East)	(Boolean)	a_5	18.45	5.53	$< 10^{-3}$
	Stand density	–	b_1	0.589	0.026	$< 10^{-3}$
	Mean diameter	(cm)	c_1	−0.1500	0.0114	$< 10^{-3}$
	Mean diameter	(cm)	c_2	0.0487	0.0062	$< 10^{-3}$
	Degrees of freedom	548				
	Power of the variance function	0.81				
	RMSE	0.497				

Table 4
Statistical parameters (estimates, standard deviations, and p-values) of the longitudinal individual basal-area-increment models for *Quercus petraea* and *Pinus sylvestris* (Eq. (8)).

Species	Factor	Unit	Parameter (Eq. (8))	Est.	SD	p-value
Quercus petraea	Slope intercept	–	γ_0	0.247	0.047	$< 10^{-3}$
	$\text{Precipitation}_{\text{Dec-July}}$	(mm)	γ_1	0.000856	0.000055	$< 10^{-3}$
	Age (on slope)	(yr)	γ_2	–	–	n.s.
	Composition	(Boolean)	γ_3	–	–	n.s.
	Interaction precipitation x composition	(mm)	γ_4	0.000205	0.000044	$< 10^{-3}$
	Threshold intercept	–	α_0	−0.55	0.54	0.31
	Age (on threshold)	(yr)	α_1	0.1061	0.0047	$< 10^{-3}$
Pinus sylvestris	Slope intercept	–	γ_0	0.769	0.092	$< 10^{-3}$
	$\text{Precipitation}_{\text{May-August}}$	(mm)	γ_1	0.00110	0.00014	$< 10^{-3}$
	Age (on slope)	(yr)	γ_2	−0.0056	0.0011	$< 10^{-3}$
	Composition	(Boolean)	γ_3	–	–	n.s.
	Interaction precipitation x composition	(mm)	γ_4	–	–	n.s.
	Threshold intercept	–	α_0	0.51	1.14	0.65
	Age (on threshold)	(yr)	α_1	0.148	0.022	$< 10^{-3}$

the age of the stand (Table 4). Fig. 2 gives a schematic representation of the model for *Quercus petraea*. The equivalent figure for *Pinus sylvestris* is given in appendix C.

3.3. Projections with climate change

Using the longitudinal model, we calculated climatic modulation (Eq. (10)) on stand growth for the three main scenarios in the IPCC climate projection (RCP 2.6, RCP 4.5, and RCP 8.5) for the Orleans forest area. To perform proper comparisons among the scenarios, we used 1950–2005 as reference years. The three RCP scenarios start at year 2006.

To check the applicability of the model for future climates, we compared the climate predictions for the three RCP scenarios with the range of the climatic conditions encountered by the trees from 1971 to 2013, the period corresponding to the calibration dataset. We compared precipitation from December to July and from May to August, which were the selected climate variables for *Quercus petraea* and *Pinus sylvestris* respectively. However, in the study area, temperature is expected to change more than precipitation in the future. Therefore, even though no temperature variables were selected in the longitudinal models, we also compared the temperatures from the dataset with future projected temperatures. We compared temperatures during the warmest period, i.e. from June to August, as higher temperatures are most likely to be detrimental to tree functioning. The figures are provided in appendix F.

We conclude that the precipitation predicted in scenarios RCP 2.5, RCP 4.6 and RCP 8.5 are in the range of the precipitation of the calibration dataset. However, the summer temperature in the scenario RCP 8.5 is over the maximum temperature of the calibration dataset from 2060 onward. The model is in extrapolation from this date for the RCP 8.5 scenario.

The modulation of growth by climate change according to the three IPCC scenarios is shown in Fig. 3 for both species. After an increase in productivity at the beginning of the 21st century, productivity will level

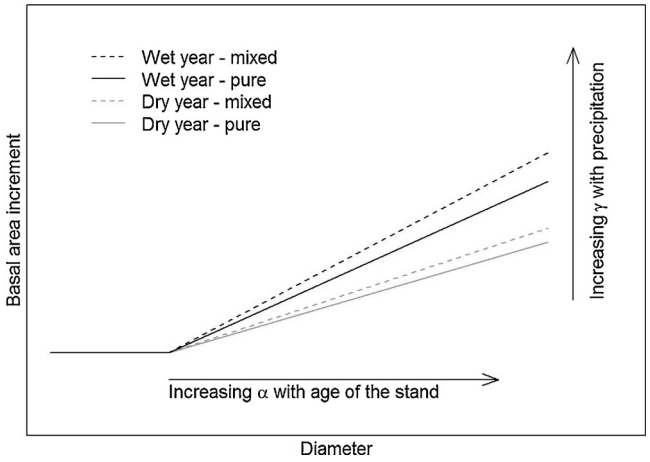

Fig. 2. Schematic representation of the longitudinal basal-area-increment model for *Quercus petraea*. The pattern is similar for *Pinus sylvestris* except that there is no mixture effect and that the slope decreases as age increases (cf. appendix C).

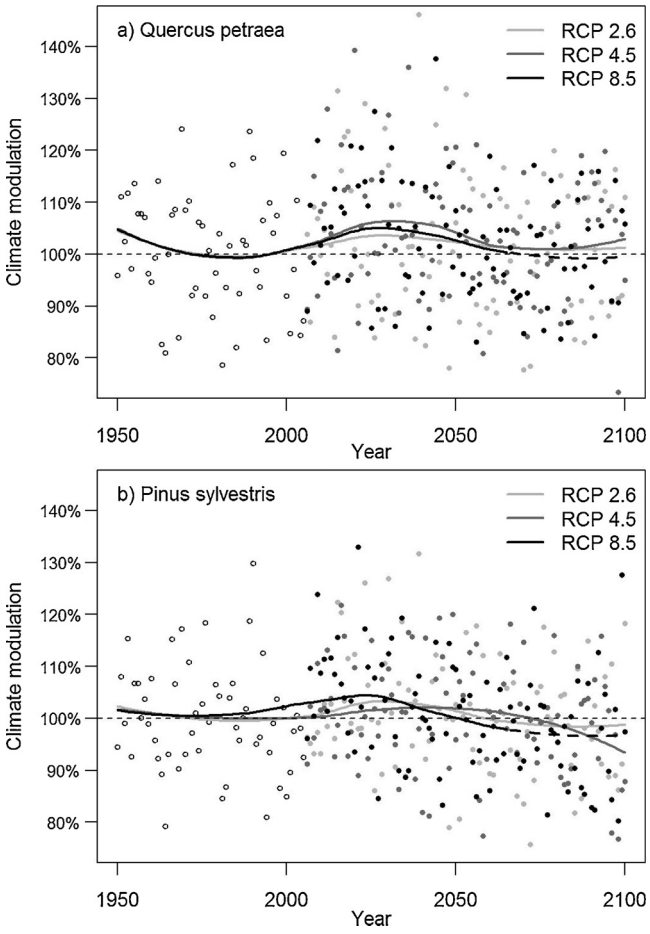

Fig. 3. Modulation in basal area growth with climate according to Eq. (10) for a) *Quercus petraea* and b) *Pinus sylvestris* according to three IPCC scenarios for the Orleans Forest area. Each point is the calculated value for the given year. Open points are historical values; solid points are IPCC projections according to the three RCP scenarios. The dashed line corresponds to smoothed model extrapolations for scenario RCP 8.5.

off or decrease slightly with little difference among the three RCP scenarios. For *Quercus petraea* mean future productivity is predicted to remain close to 100% of mean past productivity (from 1950 to 2005), whereas productivity will decrease to about 95% of mean past productivity for *Pinus sylvestris*.

4. Discussion

In this article, we developed a new type of model to predict forest stand growth that takes both silvicultural practices and annual climate fluctuations into account. We coupled a model based on NFI transversal data and a model based on tree ring measurements (longitudinal data).

4.1. Results for NFI large-scale models

Developing growth models which include biophysical factors and which are based on NFI data is becoming more common (Seynave et al., 2005; Fortin and Langevin, 2010; Vallet and Perot, 2016; Mina et al., 2018). The results we obtained for our large-scale models are close to those found in a previous study (Toïgo et al., 2015a). Here, we enlarged the spatial scale for pure plot selection in order to improve the identification and parametrization of site condition variables. On the other hand, we were more selective for mixed plots, only retaining plots at the intersection of the two species' spatial distribution. We did not find any mixture effect for this combination of species, whereas Toïgo et al. (2015a) found a positive effect of *Pinus sylvestris* on *Quercus petraea* productivity (+13.5% for a 50%-50% mixture). With their plot selection method, they retained 107 plots while we kept only 68 plots. Since in our case the number of plots was small and since our p-value for mixture effect was 0.076, we can consider the effect to be marginally significant (+9% for a 50%-50% mixture), which is consistent with Toïgo et al. (2015a).

The environmental variables influencing stand growth described in the results section are consistent with knowledge of the species' ecology.

4.2. The longitudinal models provide information on the influence of climate on growth

The size / basal area increment relationship is usually modeled using long term experiment (Dhôte, 1999; Deleuze et al., 2004; Trouvé et al., 2014). In such experiments, increment is measured with several years between measurement campaigns. This makes it difficult to link measured growth to annual fluctuations in climate. On the other hand, increment data based on tree cores make it possible to link growth to annual climate variations. Dendrochronological studies often focus on dominant trees, which account for most basal area increment in the stand. In our study, coring the trees in all diameter classes enabled us to develop stand size /basal-area increment models and to link this relationship with annual climate.

Our model can also be used to calculate resistance to climatic events, similarly to Lloret et al. (2011)'s method. These authors calculated resistance as the ratio of basal-area increment during a drought year to basal-area increment for several years before the drought event. This method needs to assume that the previous years are representative of a mean climate. With our model, we can compare the basal-area increment ratio for two different climates, thus suppressing the need for this assumption. In our results, threshold α does not depend on precipitation. Thus, the growth reduction ratio for a dry year compared to a wet year is the same for trees of all sizes, meaning that the resistance to drought does not depend on the size of the trees. The literature reveals contrasted results concerning size-dependence for resistance. Grote et al. (2016)'s review provides examples with no size dependence, other examples where larger trees declined more than suppressed trees, and still others pointing out the opposite effect.

In the longitudinal models, threshold α increases with the age of the stand for both species. This reflects the dynamics of even-aged stands: due to size asymmetry in resource competition – i.e. large trees capture a disproportionate part of the available resources (Schwinning and

Weiner, 1998) – small trees grow less as they age, until they are finally suppressed. For *Pinus sylvestris* in our study, age also had a negative influence on slope γ. This means that the competition between small and large trees decreases with age. This could be linked to the structure of the stand. In adult *Pinus sylvestris* even-aged stands, there are few height differences between trees of different diameter classes (Pérot et al., 2007). Therefore, even small *Pinus sylvestris* trees can have access to light. For *Quercus petraea*, there is a more differentiated height structure of the stand. As a consequence, small trees in adult stands have little access to light, which explains why slope γ does not decline with age for this species. Finally, *Pinus sylvestris* is shade intolerant, whereas *Quercus petraea* is rather shade tolerant (Niinemets and Valladares, 2006). If this interpretation is true, these results on slope γ could be generalized to other species using light access strategy (shade tolerance). Other interpretation, such as the age of the species with respect to the maximum age of the tree (about 200 years for pine and 500 for oak) could also be at stake.

Precipitation influenced slope γ for both species. This reflects the growth limitation for dry years. *Quercus petraea* was limited by precipitation from December of the previous year to July of the growing season, whereas *Pinus sylvestris* was limited by precipitation from May to August. This is in accordance with previous studies. *Quercus petraea* is sensitive to spring water stress whereas *Pinus sylvestris* is sensitive to summer water stress (Merlin et al., 2015; Toïgo et al., 2015b). The effect of precipitation rather than temperature was also noted by Michelot et al. (2012). We initially expected to find effects for variables reflecting water balance, i.e. not only precipitation but loss through transpiration as well. This type of variable is related to temperature. However, despite a wide range of temperature values during the 1971–2013 period (from 9.5 °C to 12.0 °C for mean annual temperature and from 16 °C to 21.4 °C for mean June to August temperature), none of the variables including temperature was better than precipitation alone, nor could any temperature variables be added to the model as a second climate variable. This may be due to the harsh soil in the Orleans forest: a sandy soil above a clay layer at about 60 cm in depth. Such a soil has low water holding capacity, making regular water input important.

4.3. Space-for-time substitution for climate

The space-for-time substitution hypothesizes that the effect of spatial variations at a given time are equivalent to the effect of temporal variations at a given place (Dunne et al., 2004).

In our study, the large-scale models (with transversal data) evidenced several effects related to different climates along geographical gradients (differences of mean climate between plots at a given time). We found a positive effect of minimum December temperature on *Quercus petraea*, which is most likely related to growing season length: the higher the minimum December temperature, the longer the growing season, and the higher the productivity. Both *Quercus petraea* and *Pinus sylvestris* were also influenced by summer climate constraints, namely July water deficit for *Quercus petraea* and maximum July temperature for *Pinus sylvestris*.

On the other hand, the longitudinal models – calibrated with temporal variation of climate on a same location – showed that amount of rainfall was the most important variable, above all other climatic variables. This variable corresponds to a water reload during winter and throughout the growing season for *Quercus petraea*, and to a growth limitation due to summer water shortages for *Pinus sylvestris*.

Even if the climatic factors revealed by the large-scale models on the one hand and by the longitudinal models on the other hand are not contradictory, they are not equivalent. This provides a counter example to the assumption that forests follow the space-for-time substitution hypothesis for climate (Elmendorf et al., 2015; Roitberg and Shoshany, 2017): the NFI models based on data with geographical induced climate variations from all France failed to reflect the annual variations of growth in the case of *Quercus petraea* and *Pinus sylvestris* in Central France. Precipitation is the important climate factor for high-frequency variations in growth (year level), and this phenomenon is not captured by large-scale models. However, we can still assume that the climatic factors revealed by large-scale data could account for the long-term tendencies of climate change, or that this space-for-time may be valid for other situations.

4.4. Growth predictions in a changing climate

Our simulations of climate modulation up to 2100 provide several findings. Overall, the modifications in climate did not drastically modify productivity for either species. At the end of the century, *Quercus petraea* had the same productivity as today. Mérian et al. (2011) already noted a low sensitivity of *Quercus petraea* to climate factors. However, for *Pinus sylvestris*, even if productivity at the end of the century remained above 95% of the reference productivity, a declining trend had started before the middle of the century. Moreover, for scenario RCP 8.5, the model provided only extrapolated results for after 2060; beyond that date, temperatures would increase up to values that were not encountered in the calibration database. The productivity decline could be more pronounced than predicted by our model for this scenario.

The patterns we obtained are closely related to the IPCC predictions for precipitation (IPCC, 2013). In the studied area (Central France), annual precipitation is not likely to change very much for any of the RCP scenarios. However, the intra-annual distribution of precipitation may change, with more water during the winter and less water during the summer. This makes all the difference between *Quercus petraea* and *Pinus sylvestris*, as the latter is influenced by May to August precipitation whereas *Quercus petraea* is influenced by December to July precipitation. Temperatures are likely to increase in summer in western France. Yet, as previously mentioned, no effect including temperature could be added to the longitudinal models, nor was temperature detected in the residuals of the final model. We can assume that for other locations, with different soil conditions leading to less growth-dependence on precipitation, the effect of temperature – as for example via potential evapotranspiration or water balance – could be observed, and would lead to greater modifications in productivity under future climate conditions.

Our results, showing a low influence of future climate on *Quercus petraea* and *Pinus sylvestris* productivity, contradict findings of Cheaib et al. (2012), especially for *Pinus sylvestris*. These authors used a multi-model comparison and predicted a huge loss of suitable areas for *Pinus sylvestris*, mainly in western France where our study was located. However, among the species they investigated, *Pinus sylvestris* had the lowest goodness-of-fit for nearly all the models used, indicating the low accuracy of their results for this species.

4.5. Interest and limitations of the coupling method

Even if our longitudinal models were tree-centered, they still reflected size-dependent competition among trees with two parameters at the stand level (threshold α and slope γ). It made it possible to benefit from tree-level information about climate and up-scale the information to the stand-level. This up-scaling made it then possible to couple the information with models developed with NFI data. This coupling method assumes that there is no interaction between the silvicultural interventions and the effects on stand growth of annual fluctuations of climate (Fernández-de-Uña et al., 2016; Alam et al., 2017).

The method has several advantages. We obtained a model with good properties: it is robust for variables related to forest management – stand developmental stage, stand density and site conditions – thanks to the wide range of NFI data used; at the same time, it is able to reflect yearly variations in climate, thanks to the longitudinal data. Moreover, the models do not require a large field effort to collect data. Indeed, NFI

data are already available in most countries and do not need additional measurements, and developing the longitudinal model required the stem slices (or tree cores) from only 108 trees for two species. However, our longitudinal data came from the Orléans forest only. New cores or stem slices need to be collected to apply our coupled model in another location. However, the large-scale model would remain the same. The limited investment required to obtain the data needed for the coupled model gives it an advantage over process-based models, if one want to generalize the results to many species and climate situations.

Nonetheless, longitudinal models depend on observed tree reactions to past climate fluctuations. Therefore, they can only provide robust results if the climate remains within the range already experienced by the trees in the calibration dataset. Some extrapolation is reasonable since all the climatic variables included in the models are linear: this linearity avoids erratic divergence outside the range of the conditions reflected in the data. However, some physiological processes could be modified if the climate deviates too far from current conditions. In particular, higher temperatures could lead to diebacks that cannot be predicted with this method. To investigate such more severe climate conditions, process-based approaches remain a better option.

Moreover, we recall that the projections presented here concern only the growth of forest stand: the assessment of the future of a tree species in the context of climate change requires the consideration of a multitude of other processes influencing forest dynamics, such as seed dispersal, regeneration, mortality, etc.

5. Conclusion

The coupling method we present in this article is a good option for climate-dependent growth models and provides robust growth predictions in the context of future climate change for the climate scenarios RCP 2.6 and 4.5. The model was in extrapolation for scenario RCP 8.5. Moreover, the method is simple and parsimonious, making it easy to generalize the results to other species and other locations. For the case study described in this article, the growth predictions of adult stand of *Quercus petraea* and *Pinus sylvestris* in western France under future climate conditions seem less worrying than in previous studies.

Acknowledgments

This study was carried out within the framework of the SATAN project (n°1660C0008, REACCTIF program) funded by the French Environment and Energy Management Agency (ADEME). The OPTMix site was installed and equipped thanks to the Région Centre Val-de-Loire, Département du Loiret and the French National Forest Office (ONF). This site belongs to the SOERE F-ORE-T, which is supported annually by Ecofor, Allenvi and the French national research infrastructure ANAEE-F (http://www.anaee-france.fr/fr/). The authors also thank the French National Forest Inventory (NFI) for providing their data free of charge (https://inventaire-forestier.ign.fr/). The English language was checked and corrected by Vicki Moore, a native English speaker. LESSEM is part of Labex OSUG@2020 (ANR10 LABX56).

Appendices Supplementary material.

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.agrformet.2018.08.021.

References

Alam, S.A., Huang, J.G., Stadt, K.J., Comeau, P.G., Dawson, A., Gea-Izquierdo, G., Aakala, T., Holtta, T., Vesala, T., Makela, A., Berninger, F., 2017. Effects of competition, drought stress and photosynthetic productivity on the radial growth of white spruce in western Canada. Front. Plant Sci. 8. https://doi.org/10.3389/fpls.2017.01915.

Assmann, E., 1970. The Principles of Forest Yield Study. Pergamon press, Oxford - New York - Toronto - Sydney - Braunschweig.

Bénichou, P., le Breton, O., 1987. Prise en compte de la topographie pour la cartographie de champs pluviométriques statistiques: la méthode Aurelhy. Colloques de l'INRA 39, 51–69.

Cheaib, A., Badeau, V., Boe, J., Chuine, I., Delire, C., Dufrêne, E., François, C., Gritti, E.S., Legay, M., Pagé, C., Thuiller, W., Viovy, N., Leadley, P., 2012. Climate change impacts on tree ranges: model intercomparison facilitates understanding and quantification of uncertainty. Ecol. Lett. 15, 533–544. https://doi.org/10.1111/j.1461-0248.2012.01764.x.

Condés, S., Vallet, P., Bielak, K., Bravo-Oviedo, A., Coll, L., Ducey, M.J., Pach, M., Pretzsch, H., Sterba, H., Vayreda, J., Río, M., 2017. Climate influences on the maximum size-density relationship in Scots pine (Pinus sylvestris L.) and European beech (Fagus sylvatica L.) stands. For. Ecol. Manage. 385, 295–307. https://doi.org/10.1016/j.foreco.2016.10.059.

Deleuze, C., Pain, O., Dhôte, J.F., Hervé, J.C., 2004. A flexible radial increment model for individual trees in pure even-aged stands. Ann. For. Sci. 61, 327–335. https://doi.org/10.1051/forest:2004026.

Dhôte, J.F., 1999. Compétition entre classes sociales chez le chêne sessile et le hêtre. Revue Forestière Française 51, 309–325.

Dufour-Kowalski, S., Courbaud, B., Dreyfus, P., Meredieu, C., de Coligny, F., 2012. Capsis: an open software framework and community for forest growth modelling. Ann. For. Sci. 69, 221–233. https://doi.org/10.1007/s13595-011-0140-9.

Dunne, J.A., Saleska, S.R., Fischer, M.L., Harte, J., 2004. Integrating experimental and gradient methods in ecological climate change research. Ecology 85, 904–916. https://doi.org/10.1890/03-8003.

Durand, Y., Brun, E., Merindol, L., Guyomarch, G., Lesaffre, B., Martin, E., 1993. A meteorological estimation of relevant parameters for snow models. Ann. Glaciol. 18, 65–71.

Elmendorf, S.C., Henry, G.H.R., Hollister, R.D., Fosaa, A.M., Gould, W.A., Hermanutz, L., Hofgaard, A., Jonsdottir, I.S., Jorgenson, J.C., Levesque, E., Magnusson, B., Molau, U., Myers-Smith, I.H., Oberbauer, S.F., Rixen, C., Tweedie, C.E., Walker, M., 2015. Experiment, monitoring, and gradient methods used to infer climate change effects on plant communities yield consistent patterns. Proceedings of the National Academy of Sciences of the United States of America 112, 448–452. https://doi.org/10.1073/pnas.1410088112.

Fernández-de-Uña, L., McDowell, N.G., Cañellas, I., Gea-Izquierdo, G., 2016. Disentangling the effect of competition, CO2 and climate on intrinsic water-use efficiency and tree growth. J. Ecol. 104, 678–690. https://doi.org/10.1111/1365-2745.12544.

Fontes, L., Bontemps, J.D., Bugmann, H., Van Oijen, M., Gracia, C., Kramer, K., Lindner, M., Rotzer, T., Skovsgaard, J.P., 2010. Models for supporting forest management in a changing environment. For. Syst. 19, 8–29.

Fortin, M. & Langevin, L. (2010) ARTEMIS-2009: un modèle de croissance basé sur une approche par tiges individuelles pour les forêts du Québec. Gouvernement of Québec (Canada), Ministère des Ressources naturelles et de la Faune, Direction de la recherche forestière. Mémoire de recherche forestière no 156. 48 pp.

Gégout, J.C., Coudun, C., Bailly, G., Jabiol, B., 2005. EcoPlant: a forest site database linking floristic data with soil and climate variables. J. Veg. Sci. 16, 257–260. https://doi.org/10.1111/j.1654-1103.2005.tb02363.x.

Grote, R., Gessler, A., Hommel, R., Poschenrieder, W., Priesack, E., 2016. Importance of tree height and social position for drought-related stress on tree growth and mortality. Trees-Struct. Funct. 30, 1467–1482. https://doi.org/10.1007/s00468-016-1446-x.

Guillemot, J., Delpierre, N., Vallet, P., François, C., Martin-StPaul, N.K., Soudani, K., Nicolas, M., Badeau, V., Dufrêne, E., 2014. Assessing the effects of management on forest growth across France: insights from a new functional-structural model. Ann. Bot. 114, 779–793. https://doi.org/10.1093/aob/mcu059.

IFN, 2011. Une nouvelle partition écologique et forestière du territoire métropolitain : les sylvoécorégions (SER). L'If 26, 1–8.

IPCC, 2013. Summary for policymakers. In: Stocker, T.F., Qin, D., Plattner, G.-K., Tignor, M., Allen, S.K., Boschung, J., Nauels, A., Xia, Y., Bex, V., Midgley, P.M. (Eds.), Climate Change 2013: The Physical Science Basis. Contribution of Working Group 1 to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

IUSS Working Group WRB (2015) World Reference Base for Soil Resources 2014, update 2015. International soil classification system for naming soils and creating legends for soil maps. World Soil Reports No. 106. FAO, Rome.

Korboulewsky, N., Perot, T., Balandier, P., Ballon, P., Barrier, R., Boscardin, Y., Dauffy-Richard, E., Dumas, Y., Ginisty, C., Gosselin, M., Hamard, J.-P., Laurent, L., Mårell, A., NDiaye, A., Perret, S., Rocquencourt, A., Seigner, V., Vallet, P., 2015. OPTMix – dispositif expérimental de suivi à long terme du fonctionnement de la forêt mélangée. Rendez-Vous Tech. - ONF 47, 60–70.

Lloret, F., Keeling, E.G., Sala, A., 2011. Components of tree resilience: effects of successive low-growth episodes in old ponderosa pine forests. Oikos 120, 1909–1920. https://doi.org/10.1111/j.1600-0706.2011.19372.x.

Mérian, P., Bontemps, J.D., Bergès, L., Lebourgeois, F., 2011. Spatial variation and temporal instability in climate-growth relationships of sessile oak (Quercus petraea Matt. Liebl.) under temperate conditions. Plant Ecol. 212, 1855–1871. https://doi.org/10.1007/s11258-011-9959-2.

Merlin, M., Perot, T., Perret, S., Korboulewsky, N., Vallet, P., 2015. Effects of stand composition and tree size on resistance and resilience to drought in sessile oak and Scots pine. For. Ecol. Manage. 339, 22–33. https://doi.org/10.1016/j.foreco.2014.11.032.

Michelot, A., Bréda, N., Damesin, C., Dufrêne, E., 2012. Differing growth responses to climatic variations and soil water deficits of Fagus sylvatica, Quercus petraea and Pinus sylvestris in a temperate forest. For. Ecol. Manage. 265, 161–171. https://doi.org/10.1016/j.foreco.2011.10.024.

Mina, M., Huber, M.O., Forrester, D.I., Thürig, E., Rohner, B., 2018. Multiple factors modulate tree growth complementarity in Central European mixed forests. J. Ecol. 106, 1106–1119. https://doi.org/10.1111/1365-2745.12846.

Niinemets, U., Valladares, F., 2006. Tolerance to shade, drought, and waterlogging of temperate Northern Hemisphere trees and shrubs. Ecol. Monogr. 76.

Pérot, T., Perret, S., Meredieu, C., Ginisty, C., 2007. Prévoir la croissance et la production du Pin sylvestre : le module Sylvestris sous Capsis 4. Revue Forestière Française 59, 57–84.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., R. Core Team, 2015. Nlme: linear and nonlinear mixed effects models. R Package Version 3. pp. 1–120. http://CRAN.R-project.org/package=nlme.

Pretzsch, H., Grote, R., Reineking, B., Rotzer, T., Seifert, S., 2008. Models for forest ecosystem management: a European perspective. Ann. Bot. 101, 1065–1087. https://doi.org/10.1093/aob/mcm246.

Pretzsch, H., Biber, P., Schütze, G., Uhl, E., Rötzer, T., 2014. Forest stand growth dynamics in Central Europe have accelerated since 1870. Nat. Commun. 5, 4967. https://doi.org/10.1038/ncomms5967.

Río, M., Sterba, H., 2009. Comparing volume growth in pure and mixed stands of Pinus sylvestris and Quercus pyrenaica. Ann. For. Sci. 66, 502.

Roitberg, E., Shoshany, M., 2017. Can spatial patterns along climatic gradients predict ecosystem responses to climate change? Experimenting with reaction-diffusion simulations. PLoS ONE 12. https://doi.org/10.1371/journal.pone.0174942.

Schwinning, S., Weiner, J., 1998. Mechanisms determining the degree of size asymmetry in competition among plants. Oecologia 113, 447–455. https://doi.org/10.1007/s004420050397.

Seynave, I., Gégout, J.C., Hervé, J.C., Dhôte, J.F., Drapier, J., Bruno, E., Dumé, G., 2005. *Picea abies* site index prediction by environmental factors and understorey vegetation: a two-scale approach based on survey databases. Can. J. For. Res. 35, 1669–1678.

Sheppard, P.R., Comrie, A.C., Packin, G.D., Angersbach, K., Hughes, M.K., 2002. The climate of the US Southwest. Clim. Res. 21, 219–238. https://doi.org/10.3354/cr021219.

Toïgo, M., Vallet, P., Perot, T., Bontemps, J.-D., Piedallu, C., Courbaud, B., 2015a. Overyielding in mixed forests decreases with site productivity. J. Ecol. 103, 502–512. https://doi.org/10.1111/1365-2745.12353.

Toïgo, M., Vallet, P., Tuilleras, V., Lebourgeois, F., Rozenberg, P., Perret, S., Courbaud, B., Perot, T., 2015b. Species mixture increases the effect of drought on tree ring density, but not on ring width, in Quercus petraea–Pinus sylvestris stands. For. Ecol. Manage. 345, 73–82. https://doi.org/10.1016/j.foreco.2015.02.019.

Toïgo, M., Perot, T., Courbaud, B., Castagneyrol, B., Gégout, J.C., Longuetaud, F., Jactel, H., Vallet, P., 2018. Difference in shade tolerance drives the mixture effect on oak productivity. J. Ecol. 106, 1073–1082. https://doi.org/10.1111/1365-2745.12811.

Trouvé, R., Bontemps, J.D., Collet, C., Seynave, I., Lebourgeois, F., 2014. Growth partitioning in forest stands is affected by stand density and summer drought in sessile oak and Douglas-fir. For. Ecol. Manage. 334, 358–368. https://doi.org/10.1016/j.foreco.2014.09.020.

Vallet, P., Perot, T., 2011. Silver fir stand productivity is enhanced when mixed with Norway spruce: evidence based on large-scale inventory data and a generic modelling approach. J. Veg. Sci. 22, 932–942. https://doi.org/10.1111/j.1654-1103.2011.01288.x.

Vallet, P., Perot, T., 2016. Tree diversity effect on dominant height in temperate forest. For. Ecol. Manage. 381, 106–114. https://doi.org/10.1016/j.foreco.2016.09.024.